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Threats to Ultraoligotrophic Marine Ecosystems

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*Remote marine areas with low productivity are amongst
the least explored and understood ecosystems of the biosphere*

1. Introduction

Marine phytoplankton account for ~1% of the world's photosynthetic biomass but for nearly half of the world's primary production (Field et al., 1998; Bryant, 2003). Water bodies are often classified on the basis of surface chlorophyll a concentrations, the photosynthetic pigment that is present in all primary producers (Table 1).

<u>Water body class</u>	<u>Chl. a (mg m⁻³)</u>
Ultraoligotrophic	<0.06
Oligotrophic	0.06-0.1
Mesotrophic	0.1-0.3
Eutrophic	0.3-1
Hypertrophic	>1

Table 1. Classification scheme based on chlorophyll a concentrations proposed by Shushkina et al. (1997).

Data from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) show that ultraoligotrophic marine areas occur within subtropical gyres at mid-latitudes and cover about 16-28% of the Earth's surface (Fig. 1) (McClain et al., 2004). Despite their low productivity, subtropical gyres account for 30-50% of global oceanic primary productivity (Karl et al., 1996). The subtropical gyres of the North Pacific, North Atlantic, South Pacific, South Atlantic and South Indian Ocean are ultraoligotrophic year-round with the lowest productivity found in the South Pacific gyre near Easter Island (Morel et al., 2010). Periods of ultraoligotrophy also occur in the Eastern Mediterranean and the North Red Sea, particularly during summer (Labiosa et al., 2003; Siokou-Frangou et al., 2010). In this chapter we compare ultraoligotrophic areas and describe the main threats to these systems.

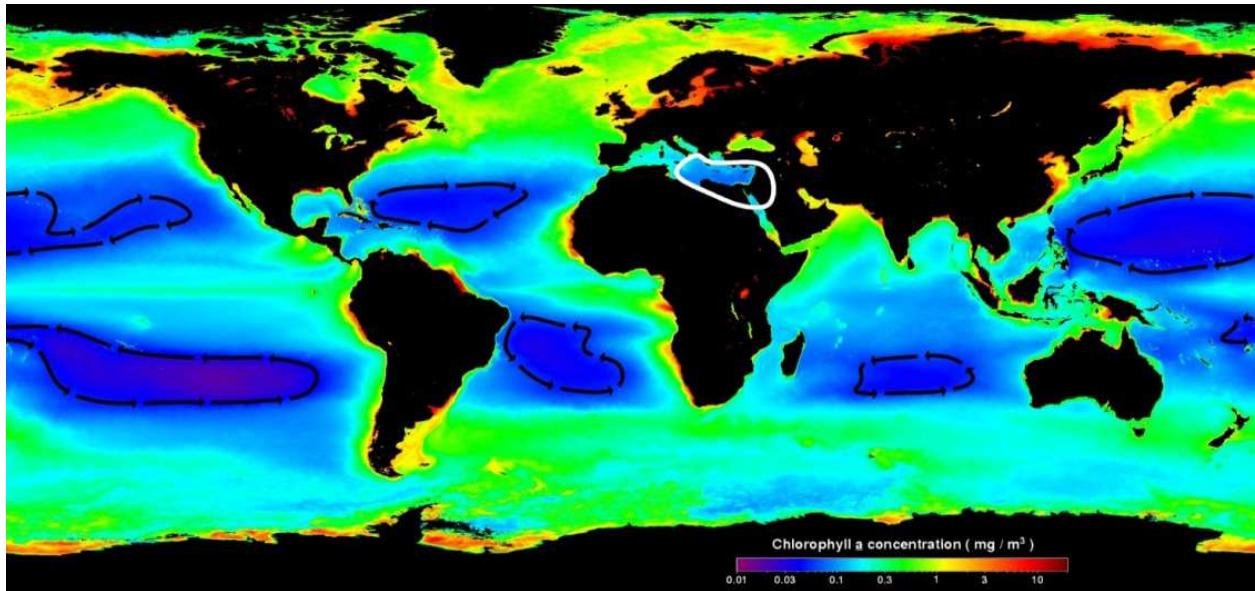


Fig. 1. World map of surface ocean chlorophyll-a concentration. Areas within black arrows and the white line indicate ultraoligotrophic ($<0.06 \text{ mg m}^{-3}$) open ocean and enclosed systems, respectively. Image from SeaWiFS Project NASA/GSFC and GeoEYE, data 1997-2010.

2. Ultraoligotrophic ecosystems

Satellite data underestimate phytoplankton productivity in ultraoligotrophic waters since light penetrates deep into the highly transparent waters, with distinct phytoplankton communities found at different depths and a peak in chlorophyll concentrations as deep as 150 m (Morel et al., 2007; Malmstrom et al., 2010). Phytoplankton sizes range from picoplankton (0.2–2 μm in diameter), through nanoplankton (2–20 μm in diameter) to microplankton (>20 –200 μm). Nutrient rich conditions favour microplankton (e.g. diatoms and dinoflagellates), which are large enough to be eaten by copepods and krill, that in turn are consumed by zooplanktivorous fish. These short, simple food webs have efficient energy transfer to larger consumers (Sommer et al., 2002). In ultraoligotrophic waters, picoplankton (Fig. 2) seem better able to acquire nutrients than large phytoplankton as they have a higher surface area to volume ratio (Raven, 1998). Picoplankton are too small to be ingested by copepods and instead are eaten by microplanktonic protists which then feed mesozooplankton (Christaki et al., 2002; Calbet, 2008) or they form aggregates that can then be consumed by crustacean and gelatinous zooplankton (Lomas & Moran, 2011). The complex food webs that occur in ultraoligotrophic waters result in less efficient energy transfer to higher trophic levels. Ephemeral phytoplankton blooms can occur in ultraoligotrophic areas and during these events herbivorous plankton proliferate rapidly thanks to short generation times (Eden et al., 2009). During blooms myriads of vertically migrating grazers such as copepods, euphausiids and gelatinous zooplankton feed higher trophic groups such as squid, fish and other vertebrates (Seki & Polovina, 2001).

Low phosphorous (P) and nitrogen (N) concentrations normally limit primary production in ultraoligotrophic systems. A spring peak in Chl. a concentrations usually occurs when longer days allow phytoplankton to thrive due to the greater nutrient availability that

follows winter mixing (Morel et al., 2010). Competition for P may have shaped the evolution of marine microbes; the dominance of picocyanobacteria genera *Prochlorococcus* and *Synechococcus* in low P environments is thought to be due in part to their ability to form lipid membranes that require less P than most other organisms (Van Mooy et al., 2006; Dyhrman et al., 2009). Picocyanobacteria and picoeukaryotes carry genes encoding for enzymes like alkaline phosphatase (AP) that hydrolyze dissolved organic phosphorous (DOP) and *PstS* genes which are related to the high-affinity uptake of phosphate (Moore et al., 2005; Martiny et al., 2009). Many plankton are able to fix N_2 although this ability can be limited by a lack of trace elements such as iron (Tyrrell, 1999; Kustka et al., 2003). The ability to fix N_2 should be ecologically advantageous in ultraoligotrophic environments where the most abundant

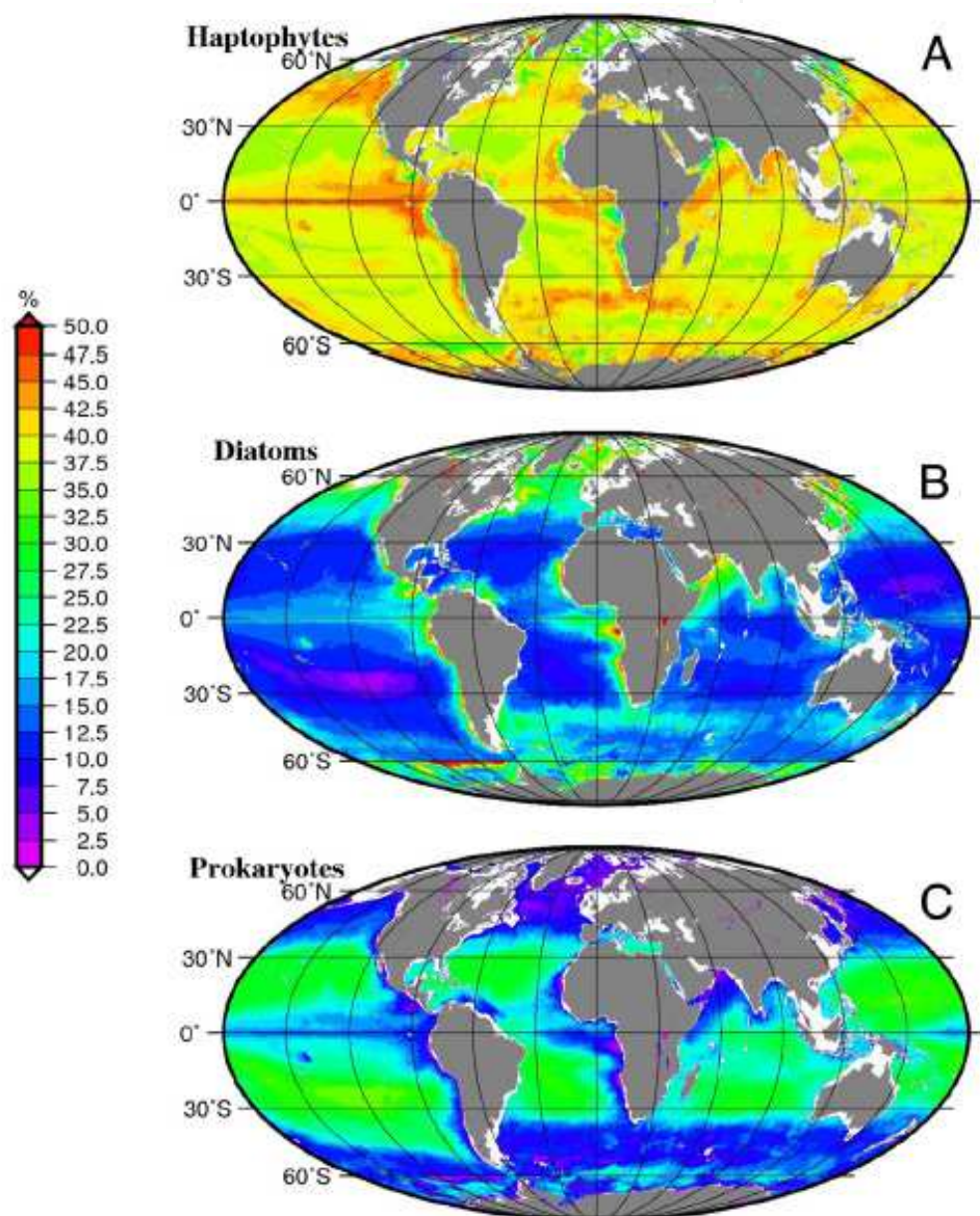


Fig. 2. Accessory pigments based on relative contribution of (A) haptophytes, (B) diatoms and (C) photosynthetic prokaryotes to total Chl. a biomass in the euphotic layer for the year 2000. Image from Liu et al. (2009).

forms of N are dissolved N_2 gas and dissolved organic nitrogen (DON). In ultraoligotrophic surface waters N_2 fixing bacteria typically have much lower abundances than non- N_2 fixing cyanobacteria and picoeukaryotes but N_2 fixation increases in importance with depth (Dekas et al., 2009). N_2 fixing cyanobacteria, such as *Trichodesmium* spp., occur in many warm, calm and oligotrophic waters (Capone et al., 1997) and are a seasonal and episodic phenomenon in ultraoligotrophic waters. So far, research efforts have focused on colonial *Trichodesmium* spp. but free trichomes, which seem more important in oligotrophic systems, have received little attention (Taboada et al., 2010). Primary production in ultraoligotrophic areas is usually dominated by unicellular N_2 fixing bacteria (e.g. *Crocospaera* and UCYN clades), non- N_2 fixing picocyanobacteria (e.g. *Prochlorococcus* and *Synechococcus* spp.) and small eukaryotes (e.g. haptophytes) (Malmstrom et al., 2010; Moisander et al., 2010). Surface-ocean microbial growth is mostly supported by regenerated production, such as DON (e.g. urea) and ammonia oxidation by nitrification which occurs in bacteria and archaea (Zehr & Kudela, 2011).

Even though photosynthetic picoplankton are dominated numerically by *Prochlorococcus* and *Synechococcus*, much of the carbon is fixed by photosynthetic picoeukaryotes such as the exceptionally diverse haptophytes (Grob et al., 2011). Picoeukaryotes are thought to contribute 30-50% of the total photosynthetic standing stock across the world ocean with their competitive success attributed to their mixed mode of nutrition as some are able to photosynthesize as well as engulf bacteria (Liu et al., 2009). Recent applications of molecular techniques demonstrate high diversity in the microbial parts of the food web (DeLong, 2009) and a previously unimagined diversity of eukaryotes (Massana & Pedrós-Alió, 2008). Even though the phytoplankton abundance is lowest in oligotrophic waters, the diversity of small-sized phytoplankton seems to peak in these areas (Cermeño & Figueiras, 2008; Kirkham et al., 2011). How such a diversity of plankton can coexist on limited resources is intriguing and was dubbed the 'paradox of plankton' by Hutchinson (1961). Explanations range from prolonged coexistence and niche segregation to mesoscale turbulence of the ocean (Roy & Chattopadhyay, 2007; Perruche et al., 2010).

2.1 Open ocean systems – Subtropical gyres

Data from monitoring stations off Bermuda and Hawaii are revolutionizing our understanding of mid-latitude gyre dynamics. Once thought of as homogeneous unchanging ocean deserts, we now know that these ultraoligotrophic ecosystems are both physically and biologically dynamic. The gyres circulate clockwise in the northern hemisphere and anticlockwise in the southern hemisphere due to the Coriolis effect. Ekman pumping (water moving to the right of the wind) and geostrophic flow cause downwelling of relatively warm surface waters at the subtropical convergence near $20^\circ - 30^\circ$ latitude (Pedlosky, 1998). The gyres have deep pycnoclines and even deeper nutriclines (e.g. nitrate, phosphate, and silicate) (McClain et al., 2004) and expand in area in summer. In most gyres Chl. a concentrations peak in spring following mixing in winter, while in the North Atlantic a secondary peak occurs at the end of September; in the North Pacific Chl. a concentration is higher during stratified conditions in the summer (Morel et al., 2010). Episodic blooms are also detected in all the gyres during stratified periods (Wilson & Qiu, 2008). The ultraoligotrophic gyres are each ecologically distinctive, as illustrated by the differences in their primary producers.

2.1.1 North Atlantic

The Sargasso Sea is probably the most studied open ocean system in the world (Steinberg et al., 2001). This subtropical gyre receives iron-rich Saharan dust (Marañón et al., 2010) but has extremely low P concentrations, possibly as a result of iron enhanced N₂ fixation (Wu et al., 2000). In January-April waves deepen the mixed layer and bring nutrients into the euphotic zone. Subsequent stratification retains nutrients in the surface waters, promoting N₂ fixation, primary production and blooms of phytoplankton such as *Trichodesmium* spp. (Taboada et al., 2010). As summer progresses the uptake of P by prokaryotes causes P limitation, although DOP is also utilised and can support ~25-30% of annual primary production (Mather et al., 2008; Lomas et al., 2010). In summer a distinct shallow-water microbial community develops in the region of lowest nutrients, with a deep chlorophyll maximum community and an upper mesopelagic community (Treusch et al., 2009). Bacteria seem to be more concentrated in the surface waters while Archaea (e.g. *Crenarchaeota*) seem better adapted in the mesopelagic layer (Schattenhofer et al., 2009). Picoplankton (*Prochlorococcus* and *Synechococcus* spp. and picoeukaryotes) dominate carbon fixation in the subsurface chlorophyll maximum, while in surface waters the nanoplankton (e.g. some haptophytes, pelagophytes, small diatoms and dinoflagellates) make significant contributions to productivity (Poulton et al., 2006). *Prochlorococcus* is twice as abundant in the deep chlorophyll zone than at the surface, but is almost absent below 200 m (Schattenhofer et al., 2009; Riemann et al., 2011). *Prochlorococcus* clades have a succession of blooms as each responds differently to seasonal changes in light, temperature and mixing. *Prochlorococcus* peak in abundance during late summer and autumn whilst *Synechococcus* is scarce then but can occasionally become more abundant than *Prochlorococcus* during winter when the Sargasso Sea is more deeply mixed (Malmstrom et al., 2010).

Even though photosynthetic picoeukaryotes are less abundant than picocyanobacteria, they cause the observed variations in Chl. a and peak in abundance during winter/spring (Riemann et al., 2011). They are extremely diverse and dominated by haptophytes and chrysophytes, neither of which was traditionally considered to be important in carbon fixation (Kirkham et al., 2011). Rates of carbon fixation are comparable to those in the South Atlantic subtropical gyre and peak during the spring blooms (Poulton et al., 2006). The North Atlantic gyre appears to be net heterotrophic in autumn and balanced in spring (Gist et al., 2009) although it may be net autotrophic annually (Kähler et al., 2010). Despite being ultraoligotrophic, the Sargasso Sea is the spawning site of Atlantic eels. We now know that the picoplankton and nanoplankton make significant contributions to carbon export into deeper zones via settling of aggregates and/or consumption of those aggregates by mesozooplankton (Lomas & Moran, 2011). In turn, mesozooplankton (e.g. heterotrophic athecate dinoflagellates and ciliates) feed copepods which may in turn be available to organisms at higher trophic levels, such as the larvae of Atlantic eels (Andersen et al., 2011).

2.1.2 South Atlantic

Much of our knowledge for the South Atlantic low nutrient gyre comes from the Atlantic Meridional Transect programme which has been undertaken semi-annually since 1995 along a 13,500km transect between 50°N and 52°S (Robinson et al., 2009). Nutrient concentrations are lower than in the North Atlantic gyre, yet the southern system appears to be more autotrophic (Gist et al., 2009). NO₃⁻ concentrations are below detection limits, and iron

concentrations are also very low, but soluble reactive P is almost an order of magnitude higher than in the North Atlantic gyre. As P is a more bioavailable nutrient source than DOP reduced APA is detected which results in accumulation of DOP (Mather et al., 2008). The microbes seem to be adapted to higher organic loading and utilize organic inputs more efficiently than heterotrophic bacteria of the North Atlantic gyre (Martinez-Garcia et al., 2010). Unlike the North Atlantic gyre, N₂ fixation is very low and is possibly limited by iron (Moore et al., 2009).

Prochlorococcus is more abundant than in the North Atlantic gyre although its contribution in the mesopelagic zone is minimal (Schattenhofer et al., 2009). SAR11 heterotrophs occur at lower abundances than in the North Atlantic gyre, but still make up about 25% of all picoplankton cells (Mary et al., 2006). Larger picoprokaryotes are found in the South Atlantic gyre compared to the North Atlantic (Schattenhofer et al., 2009). Small photosynthetic picoeukaryotes of a size <3µm seem to play a crucial role in oceanic primary production. Phylogenetic analyses using both plastid and nuclear rRNA genes reveal a high diversity especially in the members of haptophytes and chrysophytes, with the latter dominating the South Atlantic gyre and associated with higher light intensities (Kirkham et al., 2011). Chrysophytes were previously only known from freshwater systems and their significance in marine oligotrophic areas is poorly understood.

2.1.3 North Pacific

Stratification of surface waters usually inhibits marine primary productivity as nutrients become depleted in the euphotic zone. However, at ALOHA monitoring station stratification and productivity are not strongly correlated (Dave & Lozier, 2010). Presumably allochthonous nutrients maintain new production during stratified periods but it is not well understood how these nutrients are supplied. Unicellular diazotrophs frequently dominate N₂ fixation in late winter and early spring, while filamentous diazotrophs (heterocyst-forming cyanobacteria and *Trichodesmium* spp.) fluctuate episodically during the summer (Church et al., 2009). The picocyanobacteria seem well adapted to P starvation by exhibiting significant increases in APA (Moore et al., 2005). In the past, a shift from eukaryotic to prokaryotic dominance transformed the North Pacific gyre from a N-limited to a P-limited system (Karl et al., 2001). There is now molecular evidence for an increase in N-limited strains of *Prochlorococcus* which may indicate that the gyre is returning to a N-limited phase (Van Mooy & Devol, 2008).

Picophytoplankton are dominant contributors (averaging 91%) to euphotic zone Chl. a concentrations (Li et al., 2011). Cyanobacteria such as *Prochlorococcus* spp. and heterotrophic bacteria, though incapable of N₂ fixation, represent the vast majority of the total cell abundance throughout the euphotic layer (Duhamel et al., 2011). *Prochlorococcus* spp. are numerically dominant year-round. Here plankton communities can be distinguished as epipelagic, mesopelagic and bathypelagic (Eiler et al., 2011) with distinct *Prochlorococcus* clades at different depths (Malmstrom et al., 2010).

In summer Chl. a concentrations peak, the phytoplankton is supported by N₂ fixation and dominated by a few genera of large diatoms and the cyanobacterium *Trichodesmium* (Dore et al., 2008). Filamentous organisms, specifically heterocyst-forming cyanobacteria and *Trichodesmium* spp. fluctuate episodically during the summer resulting in highly variable

fixation rates, possibly triggered by mesoscale physical processes (e.g. eddies, and wind-generated waves) that input nutrient rich waters in the euphotic zone and can cause blooms in the microbial communities (Fong et al., 2008).

There is uncertainty as to whether the system is a C sink or source. Net community production is calculated to be closely balanced or slightly negative (net heterotrophic) due to tightly coupled respiration and gross community production (Viviani et al., 2011), but high oxygen concentrations below the mixed layer may be consistent with an ecosystem that is a net producer of fixed C (net autotrophic) throughout the year (Riser & Johnson, 2008).

2.1.4 South Pacific

The South Pacific gyre is the largest oceanic gyre and has the clearest waters ever described with a chlorophyll maximum as deep as 180m (Ras et al., 2008). Far from continental sources it receives the lowest atmospheric iron flux in the world (Wagener et al., 2008). Both phytoplankton and heterotrophic bacteria are limited by N within the centre gyre, but not by iron which only limits primary production at the border of the gyre (Bonnet et al., 2008). In the surface waters (<180m), NO_3^- is undetected and only trace quantities of regenerated N are found. Despite N limitation, no evidence of N_2 fixation exists and *nifH* gene abundances are extremely low compared to North Pacific gyre (Bonnet et al., 2008). This suggests that the autotrophic communities are adapted to living at low iron levels, and that the common photoautotrophic N_2 fixing organisms are not favoured due to their elevated iron quotas. In spite of strong N depletion leading to low chlorophyll biomass, the South Pacific gyre with its characteristic reduced vertical mixing can accumulate organic matter (Raimbault et al., 2008) that can sustain active regeneration processes during stratification (Raimbault & Garcia, 2007).

In the clear waters of the gyre centre autotrophic eukaryotes shift to smaller cells (<2 μm) compared to more eutrophic conditions (Masquelier & Vaulot, 2008). Flow cytometry sorting carried out in the most oligotrophic areas of the gyre revealed several novel lineages of photosynthetic picoeukaryotes such as a clade of prasinophytes. Pelagophytes, chrysophytes and haptophytes are the dominant picophytoplankton (Shi et al., 2011). Coccolithophores are an important group of unicellular calcifying haptophytes, even though at low abundances they grow down to 300m deep with maximum cell concentrations recorded between the depths of 150–200m (Beaufort et al., 2008). In addition, high taxonomic diversity is also detected in the microzooplankton tintinnids that is inversely related to chlorophyll concentration and positively to the depth of the maximum chlorophyll layer (Dolan et al., 2007). Furthermore, larger microplankton (e.g. diatoms) can adapt to the ultraoligotrophic conditions of this region by forming symbiotic relationships with other species (Gómez, 2007).

There is now growing evidence that this oceanic expanse, once thought to be net heterotrophic may be net autotrophic. The deep layers, below the euphotic zones, may be significant contributors to C fixation fuelling heterotrophic processes in the upper layer (Claustre et al., 2008). However this remains a debate; as some studies show that net community production is closely balanced or slightly net heterotrophic (Viviani et al., 2011) while data from oxygen sensors deployed on profiling floats suggest that the system is net autotrophic throughout the year (Riser & Johnson, 2008).

2.1.5 South Indian

The Indian subtropical gyre is probably the least studied gyre. Research has so far focused in the Arabian Sea (north-western Indian Ocean) and extensive regions of the oceanic gyre remain unknown. In late winter (austral summer) warm and salty subtropical water is separated from deeper water (Tsubouchi et al., 2009). This pronounced vertical stratification impedes nutrient transport into the euphotic zone leading to low seasonal NO_3^- and Si(OH)_4 concentrations that limit primary production by microplankton so that nanoplankton and picoplankton dominate productivity. The turnover rate of nanoplankton and picoplankton seems to be closely coupled to microzooplankton grazing and low nutrient concentrations (Thomalla et al., 2010).

About 90% of Chl. *a* observed at the surface and at the deep chlorophyll maximum (up to 120m depth) is attributed to the picophytoplankton fraction, while picoeukaryotes account for up to 50% of the Chl. *a* measured (Not et al., 2008). Prokaryotic *Prochlorococcus* and eukaryotic prochlorophytes, haptophytes and pelagophytes seem to dominate the oligotrophic waters of the Indian Ocean, though a large fraction of the eukaryotic genomes sampled and a significant flagellate (small phototrophic protist) remain unidentified (Not et al., 2008; Schlüter et al., 2011). Greater variation in the picoeukaryotic assemblages has been observed vertically in the upper 200m of the water column than horizontally across the entire southern Indian oceanic expanse.

2.2 Enclosed systems

The low primary production observed in open-ocean subtropical gyres relates to their isolation from freshwater and airborne nutrient sources. Few coastal regions are ultraoligotrophic, although the Eastern Mediterranean and the Northern Red Sea become ultraoligotrophic during the warmer parts of the year (Labiosa et al., 2003; Siokou-Frangou et al., 2010).

2.2.1 Eastern Mediterranean

The Mediterranean connects through the Strait of Gibraltar to the Atlantic Ocean in the west, the Bosphorus Strait to the smaller enclosed Black Sea in the northeast, and the Suez Canal to the Red Sea and Indian Ocean in the southeast. Evaporation exceeds precipitation and river run off (the main rivers are the Ebro, Rhone, Po, Danube and Nile) with surface waters increasing in salinity from west to east. Atlantic surface water enters through the Strait of Gibraltar and moves eastwards, sinking to 200-500m depth in the Eastern Mediterranean before circulating back west and exiting through the Strait after about 80-100 years and with nearly 10% more salt content (Bas, 2009).

Nutrients mainly enter the system through the Straits of Gibraltar and Bosphorus, from wind-driven Saharan dust deposits and from river discharges mainly in the north. The Eastern Mediterranean has the lowest nutrient content. Here dams have resulted in drastic reductions in freshwater flow; the Aswan dam on the Nile, for example, restricts the amount of silica entering the Mediterranean (Turley, 1999). In the Eastern Mediterranean aeolian inputs can account for 60-100% of the bioavailable N and 30-50% of the bioavailable P (Krom et al., 2010). The unusually high ratio of N to P (~28:1) observed in the Eastern Mediterranean (it can sometimes reach 105:1) is due to high N inputs from rivers and atmospheric deposition (Krom et al., 2010; Markaki et al., 2010).

In the western Mediterranean, winter mixing of surface waters with nutrient-rich deeper waters causes a winter-spring phytoplankton bloom composed mostly of diatoms with some flagellates and coccolithophorids (Goffart et al., 2002). The bloom is less-pronounced in the Eastern Mediterranean (D'Ortenzio & Ribera d'Alcalà, 2009), Chl. a concentration is $<0.1 \text{ mg m}^{-3}$ on average, with the maxima occurring in late winter - early spring and minima in late summer (Siokou-Frangou et al., 2010). In summer a sharp thermocline at 10-20m results in nutrient depletion in the surface mixed layer. During this stratified period, primary production in the Eastern Mediterranean is both N and P limited, and during the winter mixing it becomes P limited (Thingstad et al., 2005; Tanaka et al., 2011). As in other ultraoligotrophic systems, the microbial loop is in a dynamic equilibrium in which grazing pressure, competition and nutrient concentrations can shift the limiting nutrient.

The importance of N_2 fixation in the Eastern Mediterranean is under investigation. There are low concentrations of diazotrophic cyanobacteria, possibly due to P and iron limitation. The N_2 fixation rates decrease from west-east but may sustain up to 35% of the primary production in the eastern basin and can be stimulated occasionally by Saharan dust events (Bonnet et al., 2011; Ridame et al., 2011). The diazotrophic community is dominated by unicellular picocyanobacteria, although N_2 fixation has also been detected within picoeukaryotes (Le Moal et al., 2011).

Picoplankton dominate the most nutrient limited areas of the Mediterranean (Tanaka et al., 2007). Larger diatoms and dinoflagellates become abundant after intermittent nutrient pulses associated with upwelling, fronts and gyres (Siokou-Frangou et al., 2010). Over 85% of Chl. a in the eastern basin is found in ultraplankton ($<10\mu\text{m}$), that comprises cyanobacteria (*Synechococcus* spp. are dominant), chlorophytes, prasinophytes and haptophytes (Denis et al., 2009). Coccolithophores are more abundant and diverse in the eastern basin (Ignatiades et al., 2009). In summer, dinoflagellates dominate the larger plankton fraction in offshore areas of the Eastern Mediterranean whereas diatoms are more prevalent during winter mixing and in inshore waters where anthropogenic eutrophication is evident (Aktan, 2011).

Most studies describing phytoplankton biomass dynamics in the Mediterranean Sea stress that low nutrients cause low primary production (bottom-up control). However, the planktonic food webs are very efficient at minimizing C export to deeper waters, benefiting predators that control the plankton biomass (top-down control) (Siokou-Frangou et al., 2010). A P addition experiment in the Eastern Mediterranean had an unexpected outcome because Chl. a concentrations decreased while egg-carrying copepods numbers increased (Krom et al., 2005; Thingstad et al., 2005). Efficient top-down control helps explain why Mediterranean fisheries are richer than anticipated based on Chl. a and nutrient concentrations. In addition to efficient C export to pelagic top predators, benthic primary producers also play an important role in sustaining Eastern Mediterranean food webs. Highly productive benthic primary producers, such as the seagrass *Posidonia oceanica* which grow at 0 – 50m in depth (Duarte, 1991) the coralline algal habitats (e.g. maerl) which grow in low light conditions (Ballesteros, 2006) and macroalgal assemblages (e.g. *Cystoseira* forests) in the shallows form diverse and complex habitats. The Mediterranean basin ranks among 25 'biodiversity hotspots' containing about 7% of the world's marine biodiversity (Bianchi & Morri, 2000; Myers et al., 2000). Even though it covers $<0.8\%$ of the world ocean surface and is $<0.3\%$ of its volume, it is home to 4-18% of the world's recorded species,

depending on the phylum considered. Approximately 17 000 marine species occur in the Mediterranean Sea and this inventory is expanding rapidly, especially for microbes and deep sea species (Coll et al., 2010). An unusually high level of endemism is observed and the region hosts a number of species of conservation interest, such as 71 species of sharks, rays and chimaeras (Cavanagh & Gibson, 2007), sea turtles (*Dermochelys coriacea*, *Chelonia mydas*, *Caretta caretta*), nine permanent resident species of cetaceans (Reeves & Notarbartolo, 2006) and the critically endangered Mediterranean monk seal (*Monachus monachus*). The southeastern Mediterranean Sea has, on paper, the lowest species richness but this is influenced by the fact that there have been relatively sparse research efforts in this part of the Mediterranean.

2.2.2 North Red Sea

The Red Sea is thought to owe its name to intense phytoplankton blooms but they are very rare in this oligotrophic system. It connects to the Mediterranean Sea through the narrow and shallow (~8m) Suez Canal in the north and exchanges water with the Indian Ocean through the Bab el Mandeb strait (130m deep) and the Gulf of Aden in the south. There are no permanent rivers and scant rainfall so seawater entering through the Bab el Mandeb strait gets saltier as it progresses northwards. Like the Mediterranean Sea, the North Red Sea is heavily influenced by seasonal changes in physical and chemical characteristics of the water column. Oligotrophic to ultraoligotrophic conditions prevail in the northern region during the summer and autumn stratified period, while in the winter, conditions become eutrophic (Lindell & Post, 1995; Labiosa et al., 2003). The Gulf of Aqaba, at the northeast tip of the Red Sea is about 165km long, very deep (~1800m) but very narrow (max width <25km), bounded by desert and separated from the Red Sea by the shallow (240m) Strait of Tiran. Here, phytoplankton populations have a large spring bloom (with Chl. a peak at around 3 mg m⁻³) and smaller autumn bloom but in the summer levels average ~0.2 mg m⁻³ (Labiosa et al., 2003).

Although N:P ratios are lower in the summer many phytoplankton species appear to be P limited and even though P is below detection limits, APA is consistently low in the picophytoplankton fraction indicating the absence of P limitation, while larger phytoplankton express increased APA especially during the stratified period indicating P limitation (Mackey et al., 2007). N₂ fixation rates are consistently low and are higher during the deep mixing season. Diazotrophic populations are dominated by the smaller N₂ fixing organisms (Foster et al., 2009). Small unicellular cyanobacteria (e.g. *Cyanothece* spp.), are the most abundant N₂ fixing organisms, while larger filamentous *Trichodesmium* occur in surface waters especially in the winter when soluble reactive P is more abundant (Mackey et al., 2007). Inputs of aerosol NO₃⁻ to surface waters represents an important source of 'new' N in this region (Aberle et al., 2010).

The planktonic communities are characterized by low abundances and the dominance (95%) of ultraplankton (0.2-8µm) (Berninger & Wickham, 2005; Al-Najjar et al., 2007). During the summer and autumn, stratified surface waters become nutrient depleted and picophytoplankton dominate. In winter, nutrient concentrations increase and larger phytoplankton become more abundant. This pronounced seasonal succession of major taxonomic groups is observed with *Prochlorococcus* dominating during the stratified summer

period but being almost absent during the winter and chlorophytes with cryptophytes dominating during the winter mixing but being almost absent during the summer (Al-Najjar et al., 2007). Larger cells ($>8\ \mu\text{m}$) are dominated by dinoflagellates and ciliates (Berninger & Wickham, 2005). The ciliates prey on the dominant picoautotrophs so that this primary production then becomes available to metazoan grazers (Claessens et al., 2008). Stable isotope analyses revealed a complex and diverse planktonic community that included herbivores and a large variety of omnivores (e.g. non-calanoid copepods) (Aberle et al., 2010). It appears top-down and bottom-up controls operate simultaneously in the North Red Sea with small cells being controlled by grazing while larger cells (e.g. diatoms) are limited by nutrient availability (Berninger & Wickham, 2005).

Despite periods of ultraoligotrophic conditions, the Red Sea is a biodiversity and endemism hotspot (Roberts et al., 2002). The Gulf of Aqaba is characterized by very high levels of endemism, especially in the mollusc and echinoderm taxa and there are exceptionally diverse fringing reefs, steeply sloping to depths of up to 150m (Fricke & Schuhmacher, 1983).

3. Threats

The human population now exceeds 7 billion compared to around 800 million in the year 1750 and an estimated 9.4 billion by 2050 (Raleigh, 1999; United States Census Bureau, 2011). This rapid population increase has been matched with environmental degradation and global biodiversity loss. Marine litter is now ubiquitous, and resources are being exhausted at alarming rates. The major stressors of anthropogenic climate change on the world's marine ecosystems are warming, acidification and deoxygenation (Gruber, 2011) with impacts that range from decreased ocean productivity, altered food web dynamics, reduced abundance of habitat-forming species, shifting species distributions, and a greater incidence of disease (Hoegh-Guldberg & Bruno, 2010). In this section we consider how ultraoligotrophic marine ecosystems are being altered by Man, and to what extent these systems may be vulnerable to the multiple stressors that are present.

3.1 Open ocean systems

Subtropical open ocean ecosystems are far removed from human civilization yet despite this remoteness rapid changes are underway, such as ocean acidification and the accumulation of marine debris.

Climate change

Remotely-sensed ocean colour data show that ultraoligotrophic marine regions have expanded by about 15% in the past decade (Polovina et al., 2008) and that the growth of these provinces may be accelerating as they get larger (Irwin & Oliver, 2009). Significant decreases in Chl. *a* concentrations have also been recorded in most subtropical gyres (Signorini & McClain, 2011). Polovina et al. (2011) predict that ocean warming will expand the area of the subtropical biome by ~30% by 2100 due to increased water stratification and restricted supplies of nutrients to the upper water column. In such areas, large and efficient C fixing eukaryotic species are outcompeted by smaller eukaryotic and prokaryotic plankton causing productivity to fall.

During the past 100 years, rising atmospheric greenhouse gas concentrations have increased global surface ocean temperatures by $\sim 0.7^\circ\text{C}$ (Trenberth et al., 2007). The deep ocean remains relatively cool, so a density gradient is developed which increases upper ocean stratification which can lower the oxygen and nutrient contents of the water. Ocean warming and increased stratification of the upper ocean may lead to 1-7% declines in dissolved oxygen in the ocean interior with implications for ocean productivity and nutrient cycling (Keeling et al., 2010). Large expansions of the oxygen minimum zones have occurred horizontally and vertically in all tropical and subtropical oceans and it is estimated that since 1960 deoxygenated areas have increased by 4.5 million km^2 (Stramma et al., 2010). The implications of ocean warming and deoxygenation on the functioning of ultraoligotrophic systems are poorly known yet alterations in food webs can be expected since warming will favour some microbes and plankton over others (Marinov et al., 2010; Sarmiento et al., 2010).

Ocean acidification results from the uptake of anthropogenic carbon dioxide (CO_2) of which around one third is absorbed by the oceans (Sabine et al., 2004) where it reacts with water to form carbonic acid (H_2CO_3) which further dissociates into hydrogen ions (H^+) and carbonate ions (CO_3^{2-}). Increased H^+ ions lower the pH of the water. Surface waters of the oceans have been acidified by an average of 0.1 pH units compared with pre-industrial levels (Doney, 2010). Model simulations predict that ocean pH will decrease by 0.2 to 0.3 pH units by the end of the twenty first century (Orr et al., 2005). The ecological effects of ocean acidification remain uncertain yet there are widespread concerns over the effects on calcified organisms since uptake of atmospheric CO_2 leads to a decrease in carbonate concentrations and increases CaCO_3 dissolution (Riebesell et al., 2009; Rodolfo-Metalpa et al., 2011). The calcifying plankton that occur in ultraoligotrophic systems (e.g. coccolithophores, foraminiferans, and pteropods) may have a reduced ability to construct their CaCO_3 shells. Beaufort et al. (2011) for example found a significant decrease in coccolith mass at sites all over the world as $p\text{CO}_2$ concentrations increase, although there were exceptions with a heavily calcified coccolith morphotype found in some low pH areas. Biogeochemical disruptions are also possible due to ocean acidification, although the ecological effects of these remain unknown. For example experimental decreases in pH lower microbial nitrification (oxidation of ammonia into nitrite) rates (Beman et al., 2011). When stimulated by $p\text{CO}_2$, N_2 fixation rates appear to increase in filamentous non-heterocystous *Trichodesmium* spp. (Barcelos e Ramos et al., 2007) and the unicellular *Crocosphaera watsonii* (Fu et al., 2008), but decrease in heterocystous diazotrophs (Czerny et al., 2009). Changes in nitrification and N_2 fixation rates have the potential to cause fundamental alterations to the marine environment. Elevated $p\text{CO}_2$ in cultured organisms and in a few mesocosms reveal contradicting results with some prokaryotic species and communities exhibiting increased production when others are adversely impacted (Liu et al., 2010). It is clear that our understanding of the potential impacts of acidification on the overall biogeochemistry of marine waters is limited by the lack of *in situ* experiments (except in some coastal areas with CO_2 vents) and the inconsistency or lack of data for several taxa. Predicting changes to marine ecosystems is also problematic since decreasing pH/increasing CO_2 is occurring in combination with other changes such as deoxygenation and warming (Denman et al., 2011).

Marine debris

During the last 60 years, the global production of plastic has increased from 1.5 million tonnes to 265 million tonnes (Plastics Europe, 2011). The light plastic particles (e.g.

polyethylene and polypropylene) that enter water bodies then float and drift with the currents and can be transported over large distances. The subtropical gyres trap floating debris in the central slower moving water masses. Accumulating plastic was discovered in 1972 in the Sargasso Sea, with increasing amounts recorded with time, such as in the North Pacific gyre where up to 334,271 pieces per km² and a startling 6:1 biomass ratio of zooplankton to plastic were recorded (Moore et al., 2001). Similar observations have been made in the North Atlantic gyre (Law et al., 2010). Models and observations show that all five subtropical gyres are litter aggregation hotspots (Maximenko et al., 2011).

Plastic can degrade to microscopic pieces (Thompson et al., 2004) that adsorb persistent organic pollutants such as PCBs, PAHs, DDTs, PBDEs, alkylphenols, and bisphenol A (Rios et al., 2010). Planktonic plastic loaded in organic pollutants can easily be mistaken for prey and upon ingestion the pollutants bioaccumulate (Harwani et al., 2011), while the plastic remains undigested and can sometimes clog the digestive tract of the organism leading to starvation and subsequent death. Top predators have been consistently reported victims of this plastic menace; 34% of 408 dissected leatherback turtles (Mrosovsky et al., 2009), 28% of 106 dolphins incidentally captured in artisanal fisheries (Denuncio et al., 2011) and 9.2% of 141 mesopelagic fishes from 27 species in the North Pacific subtropical gyre (Davison & Asch, 2011) had plastic in their stomachs. Every albatross chick egested bolus examined from the North Pacific colonies contained plastic (Young et al., 2009). 134 different types of nets causing stomach rupturing and emaciation were found inside two stranded male sperm whales in Argentina (Jacobsen et al., 2010), and the list goes on. It is now recognized that the environmental impacts of plastic debris are wide-ranging and include among others entanglement of marine fauna, ingestion by consumers from all trophic levels including the small heterotrophic plankton, dispersal of invasive species to non-native waters, and bioaccumulation of organic contaminants (Gregory, 2009).

How the biocommunities inhabiting the deoxygenated, acidified, warm waters of the ultraoligotrophic subtropical gyres will respond to changes brought about by the 'Marine Debris Era' remains to be seen.

3.2 Enclosed systems

Due to the proximity of humans, enclosed ultraoligotrophic systems are exposed to multiple anthropogenic stressors. The benefits supplied by marine biodiversity to human health are enormous and include: i) seafood (high-quality protein, minerals and vitamin D and omega-3 fatty acids) with antioxidant properties and cardio and cancer protective effects, ii) marine organisms such as sharks, algae and sponges supply a large variety of bioactive metabolites some of which are used to treat human diseases and, iii) maritime leisure activities such as recreational provide physical and psychological effects to users such as recreational fisheries, diving, snorkelling, and whale watching (Lloret, 2010). To sustain such benefits improvements are required in the ways that we manage ultraoligotrophic seas.

The North Red Sea is a biodiversity hotspot with high levels of endemism and stunning fringing reefs that can extend to depths of 150m. Protecting the threatened coral reefs of the enclosed North Red Sea is a real challenge as there are multiple stressors already in effect. Ocean warming slows coral growth and increases bleaching events (Cantin et al., 2010). Future acidification is a significant threat that is expected to increase bioerosion and

decrease the net calcification rates (aragonite formation) of stony corals (Silverman et al., 2009; Rodolfo-Metalpa et al., 2011). Furthermore, the coral reefs of the North Red Sea attract thousands of visitors that can contribute to impacts on coral reefs (Hasler & Ott, 2008). Submerged marine litter in coral reefs of the North Red Sea with an overall mean density of 2.8 items/m² and overall mean weight of 0.31 kg/m² is another major concern (Abu-Hilal & Al-Najjar, 2009). Bioaccumulation of toxic contaminants in North Red Sea corals is high (Ali et al., 2010). Moreover, coastal development has resulted in increasing demand for freshwater. Seawater desalination plants are being constructed that discharge high salinity water often contaminated with other chemicals (Hoepner & Lattemann, 2003).

The Mediterranean coasts support a high density of inhabitants, distributed in 21 countries with a population of about 450 million (cf. 246 million in 1960), of which 132 million live on the coast (26,000 km in length). In addition, 200 million tourists per year visit Mediterranean coastal countries. During the past one hundred years, the Eastern Mediterranean has been subjected to the effects of two important events, the opening of the Suez Canal in 1869 (discussed below) and the construction of the Aswan High Dam in 1964. Before the construction of the High Dam, nutrient enrichment extended along the Egyptian coast and was detected off the Israeli coast and sometimes off southern Turkey. It provided for dense blooms of phytoplankton off the Nile Delta (Nile bloom) which in turn provided nourishment to sardines, other pelagic fishes and crustaceans. Huge declines have been observed in these fisheries in the years following the High Dam construction. Since the late 1980s the recovery of total fish landings in the region reveal that the pelagic ecosystem is adjusting but the mismatch between extremely low primary productivity and relatively high levels of fish production remains a puzzle 'the Levantine Basin Paradox' to scientists (Dasgupta & Chattopadhyay, 2004). Whether this recent increase in fisheries is due to increased fishing efforts, recovery of fish stocks or nutrient enrichments by anthropogenic activities is not yet clear.

Human activities have been reducing biodiversity of the Mediterranean Sea at all levels. The major stressors in the Eastern Mediterranean appear to be: climate change, alien species invasions, pollution, fishing impacts, eutrophication and aquaculture, and habitat loss (Claudet & Fraschetti, 2010; Coll et al., 2010; Durrieu de Madron et al., 2011). Often these stressors act synergistically and have cumulative negative impacts on a great number of taxonomic groups. The Mediterranean Sea is perhaps the most investigated marine environment in the world, however research efforts have been concentrated in the northwestern Mediterranean, so much less is known about human-environmental interaction in the ultraoligotrophic waters of southeastern Mediterranean.

Climate change

The effects of global climate change are likely to affect chemical and physical properties of the water and act synergistically with other anthropogenic stressors (Gambaiani et al., 2009). Climate change impacts in the Mediterranean may provide useful insights for potential impacts elsewhere as the region is well monitored. As in many other regions; sea temperatures are rising, acidification is underway, extreme climatic events and related disease outbreaks are becoming more frequent, native species are being displaced and invasive species are spreading (Lejeusne et al., 2010).

Increased warming across the Mediterranean increases stratification of the water column further restricting nutrient availability in ultraoligotrophic zones and is related to increased mortality of the endemic seagrass *Posidonia oceanica* (Diaz-Almela et al., 2009). Higher temperatures may disrupt juvenile life histories stages of numerous organisms (Hawkes et al., 2007; Byrne, 2011) and cause mass mortalities of adults (Garrahou et al., 2009). In addition increasing temperatures may also contribute to higher frequencies of disease outbreaks as tropical microbial pathogens are expected to spread (Danovaro et al., 2009). Rising water temperatures are altering biogeographic boundaries and leading to a progressive homogenization of Mediterranean marine biota. Changes include an increase in abundance of eurythermal species and a decrease in cold stenothermal species as well as northward species shifts and mass mortalities during unusually hot summers (Coll et al., 2010). Warm-water fish like *Thalassoma pavo*, *Sphyræna* spp., *Epinephelus* spp., *Sparisoma cretense* and, *Sardinella aurita* have spread northwestwards (Sara et al., 2005). Certain cold water species have been replaced, for example the distribution of the cave-dwelling crustacean *Hemimysis speluncola* has contracted and been replaced by *H. margalefi*, a warm water species that was previously unknown in the region (Chevaldonné & Lejeusne, 2003). Non-indigenous warm water species of algae, invertebrates and fish are enlarging their geographical ranges (Bianchi, 2007). Invasive tropical fauna and flora are most evident in the southern Mediterranean where they now form a significant portion of the biota and some outcompete native species (Lasram & Mouillot, 2009). Predicted levels of warming for the end of this century lie beyond the thermotolerance levels of the developmental stages of many metazoa (Byrne, 2011).

Ocean acidification may also alter the ecology of the Mediterranean, although the evidence to date is sparse. Israel and Hophy (2002), found that acidifying seawater to pH 7.8 with CO₂ did not adversely affect growth and photosynthesis in a wide range of Mediterranean chlorophyte, rhodophyte and phaeophyte algae whereas Invers et al. (1997) found that this level of acidification enhanced photosynthesis in the Mediterranean seagrasses *Posidonia oceanica* and *Cymodocea nodosa*. Martin and Gattuso (2009) found that the Mediterranean encrusting coralline alga *Lithophyllum cabiochae* decreased calcification when elevated pCO₂ conditions were combined with high temperatures (pH 7.8; seasonal temperature +3°C). Investigations into the effects of acidification at a natural volcanic CO₂ vent off Ischia in Italy show that seagrasses and certain seaweeds were able to benefit from the elevated CO₂ levels (Martin et al., 2008; Porzio et al., 2011) but that around 30% of the coastal biodiversity was lost at mean pH levels predicted for 2100 (Hall-Spencer et al., 2008). This is partly because ocean acidification disrupts recruitment of organisms from the plankton (Cigliano et al., 2010), and partly because peak summer temperatures increase the susceptibility of some organisms to shell and skeleton dissolution (Rodolfo-Metalpa et al., 2011). Calcareous systems such as vermetid reefs and, mussel beds, as well as deep and shallow coral communities, appear to be especially vulnerable in ultraoligotrophic regions where organisms lack food and are therefore less able to allocate resources for coping with multiple stressors. In contrast, carbon limited organisms, like seagrasses, may make use of the extra dissolved CO₂ and if their habitats are protected they may thrive due to higher photosynthetic rates.

Alien species

Warm-water species are found in the Mediterranean due to Atlantic influx, Lessepsian migration, introductions by humans and present-day sea warming (Bianchi, 2007). Most of

the 955 alien species so far recorded occur in the oligotrophic Eastern Mediterranean (Zenetos et al., 2010). About 20% of Mediterranean alien species were accidentally introduced from biofouling on ship hulls or in ballast tanks (Galil, 2009). However most (about 67%) Mediterranean alien species came from the Red Sea since the Suez Canal was opened in 1869. More than 600 tropical Indo-Pacific species have been reported entering the Mediterranean where they have established reproducing populations in the Levantine basin and beyond (Coll et al., 2010; Costello et al., 2010). The rate of invasion of species from the Red Sea into the low nutrient waters of the eastern Mediterranean is increasing due to warming. Now nearly half of the trawl catches along the Levantine coast consist of Erythrean fish, but whilst some are now targeted commercially, others are detrimental to fisheries. In Cyprus, for example, the invasive puffer fish *Lagocephalus sceleratus* is out-competing native fishes and exhausting invertebrates such as the *Octopus vulgaris* and squid; in this region several other invasive species have caused substantial shifts in coastal ecosystems (Katsanevakis et al., 2009).

Pollution

Like all coastal systems the Mediterranean Sea is affected by numerous anthropogenic contaminants, but due to its enclosed and oligotrophic nature their impacts can be exacerbated. Marine litter is a major problem in the region, causing obstruction of digestive tracts and contaminant bioaccumulation in many marine animals. Persistent organic pollutants tend to bioaccumulate and come from maritime sources, aerosol deposits, urban/industrial activity, river discharges and accumulate in harbour sediments (Gómez-Gutiérrez et al., 2007; Thébault et al., 2008).

Riverine inputs and air masses from northern and central Europe carry persistent organic pollutants that can reach the Eastern Mediterranean basin (Mandalakis & Stephanou, 2002). Large commercial harbours are situated mostly in the northwest Mediterranean and maritime traffic causes noise pollution that adversely affects cetaceans (Dolman et al., 2011). Submarine drilling for oil and gas takes place in the south with exploration now underway in the eastern Mediterranean. About 300 000 tonnes of crude oil are released into the Mediterranean every year (Danovaro & Pusceddu, 2007) and can cause environmental damage, especially when chemical dispersants are used in clean-up procedures. An oil spill in Valencia in 1990 was followed by hundreds of dead dolphins being washed up along the Spanish, French, Italian and North African shores and a year later on the beaches of southern Italy and Greece, thought to be due to disease triggered by immunosuppressants in the oil spill (Zenetos et al., 2002).

Overexploitation of resources

Industrialized fishing has severe impacts on species, habitats and ecosystems (Tudela, 2004). Several fish resources are highly exploited or overexploited (Palomera et al., 2007; MacKenzie et al., 2009). A number of other organisms are also affected by exploitation and include unwanted by-catch (accidental capture in fishing gear). Bottom-trawling is a non-selective fishing method and causes a large mortality of discarded benthic invertebrates which can induce severe biodiversity and biogeochemical changes (Pusceddu et al., 2005). Severe population declines have occurred for all top predators during the last 50 years with the Mediterranean Sea described as the most dangerous sea in the world for cartilaginous fishes (Cavanagh & Gibson, 2007). See turtles face entangling, pollution and loss of habitat.

Population declines have also been recorded among marine mammals (such as sperm whales, short-beaked common dolphins, common bottlenose dolphins, striped dolphins and monk seals) that face prey depletion, direct killing and fishery by-catch (Reeves & Notarbartolo, 2006). The Mediterranean monk seal is the most endangered seal in the world with less than 600 individuals currently surviving. Remnant populations are fragmented and declining. The species faces a number of threats (i.e. accidental entanglement, exploitation, persecution and tourism) that caused severe declines in abundance (Karamanlidis et al., 2008).

There are clearly multiple threats acting synergistically on species of the Mediterranean Sea. For example, in December 2009, a pod of seven male sperm whales stranded along the coasts of Southern Italy. It appears the cause of death was prolonged starvation not from plastic obstruction (even though plastic was found in all dissected individuals) but due to a lack of prey. High concentrations of pollutants in the tissues of the stranded animals led researchers to conclude that prolonged starvation stimulated the mobilization of highly concentrated lipophilic contaminants from their adipose tissue which entered the blood circulation and may have impaired immune and nervous functions (Mazzariol et al., 2011).

Eutrophication and aquaculture

Eutrophication in the ultraoligotrophic Eastern Mediterranean is disrupting habitats and causing community shifts. Eutrophic conditions favour opportunistic species that may increase productivity and fishery catches but may out compete the highly diverse communities of ultraoligotrophic systems. Eutrophication sources from agriculture, urbanization, river run-offs, and aquaculture. Considering the exponential human population growth and the fact that fisheries are in global decline, aquaculture efforts are predicted to increase to meet growing demand (Duarte et al., 2009).

Fin-fish farming can have a number of environmental effects on the surrounding and downstream ecosystems (Holmer et al., 2008). Dissolved wastes increase the nutrient loading of the area and particulate wastes increase sediment deposition. In the benthos sedimentation and organic loading can cause biochemical changes affecting the composition and function of benthic communities (Karakassis et al., 2000), stimulating the growth of undesirable species that produce toxic metabolic waste that can kill species of conservation significance. Large-scale *Posidonia oceanica* losses adjacent to fish farm cages have been reported across the Mediterranean (Pergent-Martini et al., 2006) including the Eastern Mediterranean (Holmer et al., 2008; Apostolaki et al., 2009).

Improved fish farm management may increase their sustainability although culturing carnivorous fish is still likely to come at environmental costs. Integrated multi-trophic aquaculture (culturing organisms from different trophic levels, mimicking natural ecosystem interactions and producing less waste than monoculture systems) may be key to environmental sustainability of aquaculture practices in ultraoligotrophic waters (Chopin, 2006; Angel & Freeman, 2009).

Habitat loss

Coastal habitats such as seagrass meadows, mollusc (oyster, vermetid and mussel) reefs, coralligenous maerl formations, and macroalgal assemblages on shallow reefs are examples of complex and highly productive ecosystems. They supply food resources, nurseries and

shelter for a large array of species that are protected by international conventions, directives and action plans. A meta-analysis of 158 experiments in the Mediterranean revealed that human activity caused adverse impacts on all habitat types. Fisheries, species invasion, aquaculture, sedimentation increase, water degradation, and urbanization can all have negative impacts on Mediterranean habitats and associated species assemblages (Claudet & Fraschetti, 2010).

Habitat destruction is considered one of the most pervasive threats to the diversity, structure and functioning of marine coastal ecosystems. The loss of habitat structure generally leads to lower abundances and species richness that usually allows opportunistic species to prosper (Airoidi et al., 2008). Habitat destruction can also impair the integrity, connectivity and functioning of large-scale processes decreasing population stability and isolating communities (Thrush et al., 2006). Continued losses of habitats to coastal development has triggered several international protective measures such as the development of Marine Protected Areas (MPAs), but their efficacy is much questioned (García-Charton et al., 2008; Montefalcone et al., 2009) as habitat loss continues apace.

Oligotrophic coastal habitats are dominated by slow growing species and intricate food webs. Habitat losses can be considered irreversible, as it would take centuries following the cessation of disturbances for ecosystems to return to their climax state.

4. Conclusions

Ultraoligotrophic marine ecosystems cover almost a third of the earth's surface and contribute significantly to global productivity and biogeochemistry. They are, however, amongst the least understood systems on this planet. Once considered to be monotonous oceanic deserts, they are now known to have highly dynamic physical and biological properties with extremely diverse and vertically-distinct planktonic communities.

There is increasing evidence that these systems may be net autotrophic. The water column is dominated by the smallest eukaryotic and prokaryotic picoplankton, which seem well adapted for surviving in oligotrophic conditions. Adaptations range from niche segregation through prolonged coexistence, symbiotic associations, mixed modes of nutrition, lower cellular nutrient requirements, genes encoding for enzymes that regenerate nutrients from allochthonous sources, genes involved in high affinity uptake of nutrients and efficient nutrient uptake due to large surface: volume ratios. Unicellular cyanobacteria and extremely diverse picoeukaryotes dominate primary production in the deep euphotic zones of ultraoligotrophic waters. This production is channelled through the microbial food web (e.g. small ciliates and nanoflagellates) to vertically-migrating gelatinous and crustacean zooplankton and then to higher trophic levels. Phytoplankton blooms mainly occur after winter mixing events but sporadic blooms can occur during the stratified periods. Such blooms can favour larger planktonic species that in turn may sustain large predators (e.g. leatherback turtles, elasmobranchs, cetaceans, tunas and billfishes).

Environmental metagenomics has revealed the high biodiversity observed in ultraoligotrophic marine systems, although the causes for this high biodiversity remain puzzling (Roy & Chattopadhyay, 2007). In the Eastern Mediterranean and North Red Sea biogenic engineers such as corals, seagrasses, and macroalgae form habitats that are biodiversity hotspots of international commercial significance. Exponential growth in the

human population has resulted in multiple stressors that act synergistically in the marine environment reducing biodiversity. We believe that in ultraoligotrophic environments, where resources are scarce, organisms are particularly vulnerable to multiple stressors. Climate change is underway and its impacts may continue for many millennia after cessation of anthropogenic CO₂ emissions (Tyrrell, 2011). Warming increases stratification that keeps nutrients below the thermocline. Deoxygenated regions are expanding and acidification may impair ecological functioning (Byrne, 2011). Predictions for 2100 include substantial changes in biogeochemical processes and the extinction of many tropical coral reefs (Silverman et al., 2009). In addition to climate change, marine litter continues to accumulate in ultraoligotrophic subtropical gyres where it is physically degraded to microscopic pieces adsorbing persistent organic contaminants from the surrounding water. Plastic has been found in many consumer species ranging from copepods to large mammals. It may cause starvation, contaminant bioaccumulation, alien species transportation and entanglement. Enclosed ultraoligotrophic systems face additional threats due to their close proximity to Man. Toxic pollutants bioaccumulate and impair the normal physiological functions of organisms causing for example, cetacean strandings. Invasive alien species are spreading and are competing, predating and infecting indigenous species and altering ancient food webs. Marine fish stocks are overexploited with most top predators in decline. Eutrophication decreases water quality which can add pressure on coastal systems subjected to habitat loss and degradation. It is clear that past methods have failed to ensure environmental sustainability yet there are several reasons to be optimistic.

It is now realized that marine ecosystem degradation is a global concern. International efforts to reduce rates of biodiversity loss have led to numerous agreements, conventions or other legal instruments that are coming into force. Such international agreements form the basis of long-term collaboration that is necessary for improved environmental management. For example, the Kyoto Protocol came into force on 2005 and commits the 191 member states to tackle the issue of global warming by reducing greenhouse gas emissions. Annex 1 countries pledged to reduce their emissions by 5.2% from 1990 levels by the end of 2012. The United Nations Convention on the Law of the Sea (UNCLOS) signed by 161 countries helps control pollution and set guidelines for the protection of the environment and the management of marine natural resources in the world's oceans. Inter-governmental organizations, like the International Commission for the Conservation of Atlantic Tunas (ICCAT), are charged with the conservation of stocks of highly migratory species. In Europe, the Marine Strategy Framework Directive aims to achieve healthy waters by 2020 with an unprecedented level of cooperation between countries in developing a network of MPAs. Monitoring of environmental quality, biodiversity and long-term changes in community structure through an international coordinated network of MPAs is an approaching reality. Cautious use of Integrated Coastal Zone Management and Environmental Impact Assessments can help slow the rate of coastal environmental degradation. International partnerships like the Global Ocean Biodiversity Initiative (GOBI) are promising and the identification of Ecologically or Biologically Significant Areas (EBSAs) in the open oceans and deep seas is well underway. It is clear that these international efforts are required to slow the rates of marine environmental degradation.

There are now ample examples where interventions have had positive environmental outcomes. A primary goal among nations should be to raise awareness of effective marine environmental protection. For example, the most viable option to reduce litter is to reduce

its production in the first place and then to improve reuse and recycling through enhanced environmental awareness (Thiel et al., 2011). There is now scientific clarity that ocean warming, acidification and deoxygenation are underway due to CO₂ emissions so the primary mitigation strategy is to reduce these emissions (Gruber, 2011). There are reasons to be optimistic about improved management of ultraoligotrophic systems as a growing awareness of their value is being accompanied by shifts towards more sustainable ways of obtaining resources (e.g. marine renewables) and dealing with wastes (e.g. carbon capture and storage).

Change is underway...

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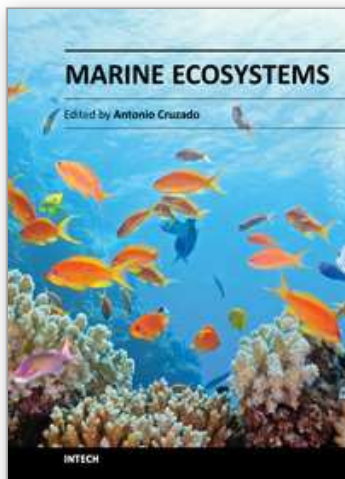
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Marine ecosystems, a very wide topic, includes many different processes, groups of organisms and geographical peculiarities. The objective of this book is to present various topics of great importance for understanding the marine ecosystems, what they are, how they work and how we can model them in order to forecast their behaviour under changing conditions. They have been thoroughly reviewed and accepted for publication. The chapters cover aspects such as: Threats to ultraoligotrophic marine ecosystems (Ch. 1); Modelling the pelagic ecosystem dynamics: the NW Mediterranean (Ch. 2); The marine ecosystem of the Sub-antarctic, Prince Edward Islands (Ch. 3); Meiofauna as a tool for marine ecosystem biomonitoring (Ch. 4); Chemical interactions in Antarctic marine benthic ecosystems (Ch. 5); An Interdisciplinary Approach on Erosion Mitigation for Coral Reef Protection- A Case Study from the Eastern Caribbean (Ch. 6); A revisit to the evolution and ecophysiology of the Labyrinthulomycetes (Ch. 7); Seabed mapping and marine spatial planning: a case-study from a Swedish marine protected area (Ch. 8); Management strategies to limit the impact of bottom trawling on VMEs in the High Seas of the SW Atlantic (Ch. 9); Hydrocarbon contamination and the swimming behavior of the estuarine copepod *Eurytemora affinis* (Ch. 10), and Interactions between marine ecosystems and tourism on the Adriatic and Mediterranean (Ch. 11).

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